Enhancement of the Response of Rock Crabs, *Cancer irroratus,* to Prey Odors following Feeding Experience

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Abstract. The rock crab, *Cancer irroratus* Say, uses chemically mediated learning in the search for food. Rock crabs are opportunistic benthic predators and scavengers. Observations indicate that although they eat a variety of items, they are more sensitive to, and prefer, odors of food items that they have been eating. We found that *C. irroratus* is more responsive to a familiar food source than to an unfamiliar one and can distinguish between the odors of two different prey after being fed one species for an extended time. Initial preferences for two mytilid bivalves, *Mytilus edulis* and *Geukensia demissa,* were determined in a Y-maze. Crabs were then fed only one of the mussel species for 28 days and retested, using sequential and simultaneous presentations, for their responses to familiar and unfamiliar prey odors. Crabs increased their responses to familiar prey odors, but not to unfamiliar odors. In foraging tests, crabs ate *M. edulis* more often regardless of the species to which they had been familiarized.

Introduction

A search image can be defined as a perceptual filtering mechanism learned from experience. It may be only a transitory improvement in perceptual ability, but this selective attention can increase the possibility of stimulus detection (Bond and Riley, 1991). In foraging behavior selective attention results in certain prey characteristics being discriminated by a predator, facilitating more efficient foraging. Search images increase accuracy and decrease response time because the predator requires less information about the prey and becomes more efficient in locating it (Lawrence, 1985a).

Search images, originally postulated for visual stimuli (Croze, 1970; Pietrewicz and Kamil, 1979; Lawrence, 1985a, b) could also be associated with chemical stimuli (Atema *et al.,* 1980; Atema and Derby, 1981; Derby and Atema, 1981). In the aquatic environment, especially in the absence of light, chemical signals may be the best cues for information about the surrounding environment. Organic molecules are part of the ambient milieu, and an organism must sift out extraneous "noise" to find the information needed for foraging, predator avoidance, and mating (Zimmer-Faust, 1991).

Chemosensory cues play a major role in agonistic (Karavanich and Atema, 1998), sexual (Gleeson, 1980), host-finding (Atema and Derby, 1981), and foraging (Pearson and Olla, 1977) behaviors in crustaceans. Experience influences an animal's response to those cues. Derby and Atema (1981) demonstrated that after lobsters (*Homarus americanus*) fed on a specific prey, their sensitivity to that prey odor increased, and they developed a preference for that particular prey. The rocky shore gastropod *Nucella lamellosa* can discriminate between predatory and nonpredatory crab effluents (Marko and Palmer, 1991), and the nudibranch *Aeolidia papillosa* can distinguish between odors from a learned prey anemone and five other possible prey anemones (Hall *et al.,* 1982). Yellowfin tuna (*Thunnus albacares*) became more sensitive to specific fish odors after feeding on that prey for a period of time, but lost their sensitivity after a few weeks without reinforcement (Atema *et al.,* 1980). In predatorily naïve postlarval lobsters, responses to metabolites of *Cancer irroratus* and *Mytilus edulis* (normal lobster prey) were lower than in field-collected adult lobsters that may have had experience with those prey (Daniel and Bayer, 1987a). When naïve lobsters were fed amphipods or clams, those fed amphipods developed stronger responses to amphipod and not to clam metabolites, but those fed clams did not develop strong responses to either prey (Daniel and

Bayer, 1987b). In theory, search images need to be rein-forced (Atema *et al.*, 1980; Atema and Derby, 1981), and their strength may vary with experience and with the avail-ability and palatability of the food (Gendron, 1986).

Many studies have tested the role of chemoreception in foraging, but few have centered on search images. We examined search images and foraging behavior in the rock crab *C. irroratus* preying on the bivalve mussels *Geukensia* and *Mytilus*. These two groups of mussels occur in the range of *C. irroratus*, are frequently taken as prey items (Stehlik, 1993), and have similar physical characteristics. *Mytilus* is found on hard substrates in the tidal zone, and individuals located close to shore are known to be eaten by rock crabs (Drummond-Davis *et al.*, 1982; Stehlik, 1993). *Geukensia* is found in soft substrates in tight clumps attached to marsh grasses, and is less likely to be encountered by a crab. No data are available on innate prey preferences in *C. irroratus*.

Using effluents from these two species, we examined changes in the responsiveness and sensitivity of crabs to prey. Chemoreceptors on various body parts appear to in-fluence behaviors such as walking, searching, and dactyl grasping, and these actions are dependent upon the concen-tration of the stimulus (Derby and Atema, 1982). The po-sition and movements of these structures are good indicators of the sensitivity to food odors (Derby and Atema, 1981). We determined a baseline response for rock crabs, famil-iarized them with a single prey, and retested them to deter-mine if there were acquired or changed responses to familiar and unfamiliar odors.

Materials and Methods

Rock crabs were collected by local watermen using traps off the coast of Delaware and Maryland and by the inves-tigators at Chincoteague on Assateague Island, Virginia. Ribbed mussels, *Geukensia demissa*, between 2 and 6 cm, were collected from salt marsh environments in Girdletree, Maryland, and Chincoteague, Virginia. Blue mussels, *Myti-lus edulis*, between 2 and 6 cm, were collected on the rock jetty at the Ocean City, Maryland inlet.

Maintenance conditions

A recirculating, biologically filtered saltwater system was used for tests. The water temperature was $11° \pm 3°C$, the salinity was 32 to 35 ppt, and the photoperiod was 12 h light:12 h dark. Crabs were kept in 40-l tanks (50×25 cm), two per tank, with an acrylic plastic divider separating them to prevent aggression and to enable staggered feeding. They were acclimated to laboratory conditions for 1–2 weeks and fed a diet of squid (*Loligo* sp.) every other day. Mussels were housed in an isolated 80-l tank equipped with a power filter. Fresh mussels were collected every week. The water in the mussel tank was kept at $15° \pm 2°C$ and the salinity at 33 to 34 ppt.

The Y-maze

Crabs were tested in a $92 \times 33 \times 20$ cm acrylic plastic Y-maze containing 55 to 60 l of salt water. A piece of acrylic divided the top 50 cm of the maze into two arms (see Fig. 1, Rebach, 1996). A dual-head MasterFlex peristaltic pump (Cole-Parmer #7553.20) delivered liquids through plastic tubing to a 2.5-cm hole in either arm of the Y-maze at the rate of about 0.33 l min^{-1}. A concentration gradient was established, with the odor becoming more dilute at the drain located at the base of the maze. In dye trials using methylene blue, the average dilution at the base of the maze was determined by spectrophotometer to be 13.6% that of the original concentration. These trials indicated that odor reached the crab within 3 min, with little mixing. In pre-liminary trials, crabs responded to odor within a few min-utes of its reaching them. Each test lasted 10 min during which the observer recorded, from a blind, crab location in the maze and behaviors exhibited.

Mussel effluent

Mussel effluent was produced daily by placing live mus-sels (equivalent to 10 g soft tissue l^{-1}) in seawater for 10 h (Derby and Atema, 1981). Mussels were checked weekly for reproductive condition to ensure that effluents would be consistent in character.

Behaviors

We adapted methods used by Derby and Atema (1981) for tests of chemoreceptive sensitivity and measured changes in behavior in the Y-maze that reflected changes in sensitivity. An approach to the source of the effluent was defined as a high-sensitivity behavior. Low sensitivity was characterized by the following behaviors:

1. Chela raise—claws lifted beyond normal position.
2. Antennule burst—flicking rate increased suddenly.
3. Antennule wipe—antennules groomed, usually with third maxillipeds. May occur in bouts. Wipes occur-ring within 5 s of each other were considered to be one wipe.
4. Maxilliped wave—third maxillipeds moved slowly back and forth without touching one another.
5. Maxilliped wipe—third maxillipeds rubbed against each other within a 5-s period.
6. Shift—body position changed.
7. Body raise—body raised up on dactyls.
8. Fanning—rapid movement of second maxillipeds along with third maxillipeds opened widely to ex-pose mouth parts.

An approach was scored when a crab crossed a line 8 cm from the inlet flow at the end of an arm of the Y-maze before a 10-min run was completed. Crabs began the ex-

periment at the base of the maze. If an approach did not occur during a test run, the low-sensitivity behaviors were used for scoring. In every run, each occurrence of a behavior other than an approach was counted as one unit (Derby and Atema, 1981). Totals for each crab were then averaged to determine a mean frequency. The higher the value, the more sensitive the crab was, or had become, to the prey odor. Scores were obtained for each crab tested before and after training was complete.

Initial response to mussel effluent

Sixteen crabs were fasted for 24 h and then tested. In control tests, seawater was used on both sides of the Y-maze. Each crab was allowed to acclimate in the maze for 8–12 h and then tested with effluent and a seawater control. This was repeated for the other mussel species about 10 h later. Initial response tests were completed within 24 days.

Familiarization with a specific mussel odor

After testing crabs for their initial response, training began. Eight crabs were fed *Geukensia* and eight *Mytilus* for a period of 28 days. Crabs were fed whole mussels *ad libitum* during the training period. The average number of mussels eaten each day was recorded.

Response to odors in sequential presentation after familiarization

Familiarized crabs were retested as in the first experiment. The tests began with a post-familiarization seawater control using seawater in both arms of the Y-maze. Responses to the two prey effluents (familiar and unfamiliar) were recorded based on sequential presentation; each prey odor was tested against a seawater control. Approaches were recorded when they occurred; if no approach occurred, low-sensitivity behaviors were scored.

Response to odors in simultaneous presentation after familiarization

Familiarized crabs were retested for preference between the two effluents. Odors were presented simultaneously without a seawater control. Distinguishing which odor elicited heightened behavioral responses was not possible in this test, so only approaches were scored.

Influence of experience on mussel selection

A foraging test was performed using live prey in 40-l tanks. Five equal-sized mussels of each species were randomly positioned in the tank and buried to about 66% of their length in a calcite substrate to make them tactually cryptic. Crabs were allowed to forage for 12 h, and each test was videotaped. The total number of mussels handled and

the species handled first, eaten first, or rejected after being handled were recorded. Mussel shells were marked with small spots of white epoxy to make them easier to see during videotape analysis.

Analysis of data

Initial scores for responses to seawater, the *Mytilus* and *Geukensia* effluents, and the sequential presentation test results were compared using the Friedman test (Systat 8.0, SPSS Inc., Chicago, Illinois). Responses to familiar and unfamiliar odors for each familiarization group were compared with the Wilcoxon signed rank tests. (Systat 8.0). Differences between means were determined with Bonferroni post hoc analysis (Systat 8.0). Mussel selection data from the foraging test was analyzed using a Wilcoxon signed rank test, a Mann-Whitney test with tied ranks, and a chi-square 2×2 contingency table (Zar, 1984).

Results

Behavioral observations

Crabs responded to effluents within 2 to 3 min. Those that did not approach responded by displaying lower sensitivity behaviors. Typically, crabs flicked their antennules slowly or intermittently, with occasional bursts, before odors reached them. A burst, with maxilliped or antennule wipes, occurred when the effluent reached the crab. Within 5 min, chela waves and raises occurred, and crabs began to move. Antennule flicks pointed in the direction of movement. These behaviors continued until tests were concluded.

In a typical approach, the initial behavior was similar to that of a non-approach. At about 5 min, crabs began walking towards the effluent. Upon reaching the end of the maze, they often grabbed the inflow hole with their chelae. In some simultaneous presentation tests, crabs entered one arm of the maze, turned back, and then proceeded down the other side, through which the familiar effluent flowed.

Initial response to mussel effluent

Figure 1 shows the responses of 16 crabs to mussel effluent before the crabs were familiarized with other mussel species. The Friedman test revealed no differences between the responses to the seawater control and to the *Mytilus* or *Geukensia* effluents ($P > 0.05$, Table 1).

Familiarization with mussel odor

Familiarization periods began after initial responses were obtained. Crabs were fed their assigned species of mussel *ad libitum*. At first, crabs consumed 6 to 8 mussels a day, although within 4 weeks this decreased to 2 to 3 mussels a day, especially those fed *Geukensia*. During familiarization, crabs exhibited periods of increased activity. Usual behav-
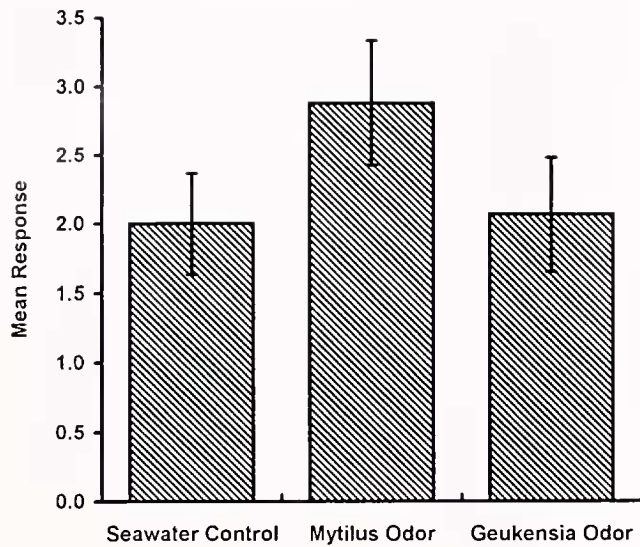
Figure 1. Comparison of mean (±SEM) frequencies for the initial tests for responses to odor. No differences were found between responses to odors.

iors consisted of climbing tank walls, eating, and resting with intermittent antennule flicking.

Response to odors in sequential presentation after familiarization

Two crabs, fed with blue mussel, made approaches to their familiar effluent. One crab, fed with ribbed mussel,

died during the familiarization period; another crab, fed with blue mussel, stopped eating 3 weeks into the training period. Activity scores from the remaining 12 crabs were analyzed for increases in sensitivity to familiar prey odor. A Friedman test determined that responses were significantly different ($P < 0.01$, Table I) to pre-familiarization seawater, post-familiarization seawater, unfamiliar mussel effluent, and familiar effluent (Fig. 2). Bonferroni post hoc analysis demonstrated that the response to familiar effluent was significantly greater than to all of the other water samples and effluents ($P < 0.01$). No other significant differences were found (Table I).

Figure 3 shows the responses of crabs familiarized with *Mytilus* or with *Geukensia* to familiar and unfamiliar odors. Wilcoxon signed ranks tests determined that responses differed to familiar and unfamiliar odors for both familiarization groups ($P < 0.05$, Table I). Bonferroni post hoc comparison determined that each familiarization group could detect the difference between the odors that were familiar and the odors that were unfamiliar to their training groups ($P < 0.01$, Table I). There was no difference in the response of each of the familiarization groups in their ability to distinguish their own familiar or their own unfamiliar odors ($P > 0.05$).

Response to odors in simultaneous presentation after familiarization

Of the 8 crabs familiarized with *Mytilus*, 4 approached familiar prey effluent; of the 8 familiarized with *Geukensia*,

Table I

Responses to effluents

| Odors compared	Method of comparison	n	P value
Initial odors	Friedman statistic (Fig. 1)	16, 16, 16	>0.05
Pre-familiarization and post-familiarization seawater, familiar and unfamiliar mussel effluents	Friedman statistic (Fig. 2)	12, 12, 12, 12	<0.01
familiar *vs.* unfamiliar effluents	Bonferroni test (Fig. 2)	12, 12	<0.01
familiar effluent *vs.* post-familiarization seawater	Bonferroni test (Fig. 2)	12, 12	<0.01
familiar effluent *vs.* pre-familiarization seawater	Bonferroni test (Fig. 2)	12, 12	<0.01
unfamiliar effluent *vs.* pre-familiarization seawater	Bonferroni test (Fig. 2)	12, 12	>0.05
unfamiliar effluent *vs.* post-familiarization seawater	Bonferroni test (Fig. 2)	12, 12	>0.05
Familiar and unfamiliar odors–familiarized w/ *Mytilus*	Wilcoxon signed ranks test (Fig. 3)	5	<0.05
Familiar and unfamiliar odors–familiarized w/*Geukensia*	Wilcoxon signed ranks test (Fig. 3)	7	<0.05
familiar *vs.* unfamiliar odors–familiarized w/ *Mytilus*,	Bonferroni test (Fig. 3)	5, 5	<0.01
familiar *vs.* unfamiliar odors–familiarized w/*Geukensia*	Bonferroni test (Fig. 3)	7, 7	<0.01
unfamiliar odor–familiarized w/*Geukensia* *vs.* unfamiliar odor–familiarized w/ *Mytilus*	Bonferroni test (Fig. 3)	7, 5	>0.05
familiar odor–familiarized w/*Geukensia* *vs.* familiar odor–familiarized w/ *Mytilus*	Bonferroni test (Fig. 3)	7, 5	>0.05
Mytilus eaten *vs.* *Geukensia* eaten	Wilcoxon signed ranks test	14	<0.05
Mytilus rejected *vs.* *Geukensia* rejected	Wilcoxon signed ranks test	9	>0.05
No. mussels eaten–familiarized on *Mytilus* or *Geukensia*	Mann-Whitney tied ranks (Fig. 4)	7, 7	>0.05
No. mussels rejected–familiarized on *Mytilus* or *Geukensia*	Mann-Whitney tied ranks (Fig. 4)	7, 7	>0.05
Species eaten *vs.* familiarization species	2 × 2 chi-square (Fig. 4)	14	>0.05
Species rejected *vs.* familiarization species	2 × 2 chi-square (Fig. 4)	14	>0.05
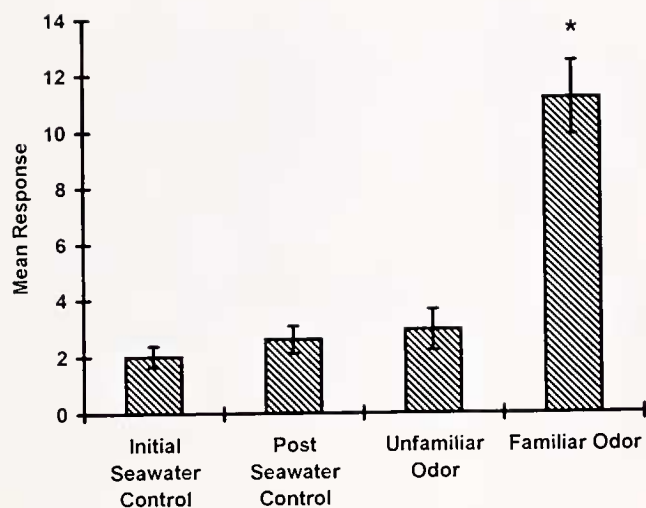
Figure 2. Comparison of mean (±SEM) frequencies of initial and post-familiarization control tests, and tests of familiar and unfamiliar odors after familiarization. No differences were found between responses to seawater controls and unfamiliar odors, but responses to familiar odors were significantly greater than to unfamiliar odors and controls (as indicated by an asterisk).

Low-sensitivity scoring could not be used because it would not have been possible to determine which odor was influencing the behavior.

Influence of experience on prey selection

Within 15 min of being placed in the tanks, crabs probed the calcite substrate with their dactyls, attempted to climb tank walls, or walked around. During this period, all crabs touched and moved both species of mussels.

More *Mytilus* (45) were eaten than *Geukensia* (19), but about the same number of mussels of both species were rejected (*Mytilus*, 13; *Geukensia*, 14). A Wilcoxon signed ranks test determined that, overall—regardless of familiarization group—significantly more *Mytilus* were eaten than *Geukensia* ($P < 0.05$), but there was no difference in numbers of *Mytilus* or *Geukensia* rejected ($P > 0.05$) (Table 1).

Figure 4 compares the species of prey eaten and rejected by crabs in the two familiarization groups. Crabs familiar with *Geukensia* cumulatively ate 21 *Mytilus* and 5 *Geukensia*, and rejected 11 *Mytilus* and 11 *Geukensia*. Crabs familiar with *Mytilus* ate 24 *Mytilus* and 14 *Geukensia*, and rejected 2 *Mytilus* and 3 *Geukensia*. In all cases, *Mytilus* was handled first and eaten first. Both groups of crabs handled about the same number of mussels (43 for *Mytilus*-familiarized crabs and 48 for *Geukensia*-familiarized crabs).

A Mann-Whitney test with tied ranks determined that there was no significant difference in total mussels, regardless of species, eaten ($P > 0.05$) or rejected ($P > 0.05$), between crabs familiarized with *Mytilus* and crabs familiarized with *Geukensia* (Table 1).

I approached unfamiliar effluent. These tests failed to yield significant responses because only approaches were scored. The 11 crabs that did not approach during the simultaneous presentation exhibited increased sensitivity, as in the sequential tests. These crabs began to search soon after the odor reached them; they raised chela and walked upcurrent and downcurrent, but they failed to make an approach.
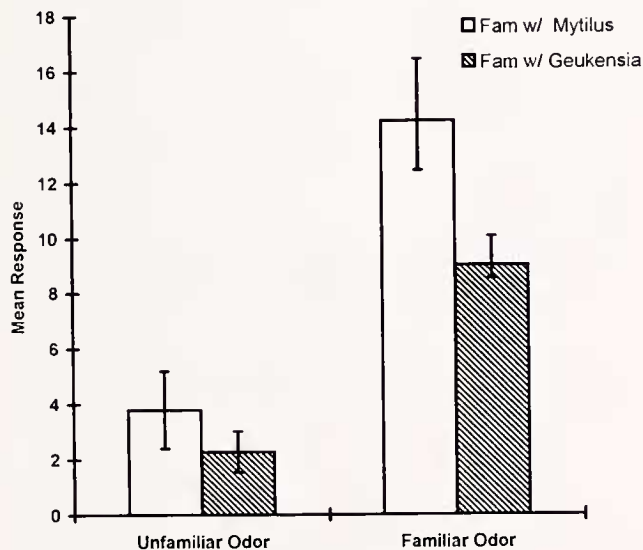

Figure 3. Comparison of mean (±SEM) frequencies between familiarization groups. No differences were found in unfamiliar odor responses between familiarization groups. Differences were found in familiar odor responses. Abbreviations: Fam w/ *Mytilus* = Familiarized with *M. edulis*; Fam w/ *Geukensia* = Familiarized with *G. demissa*.
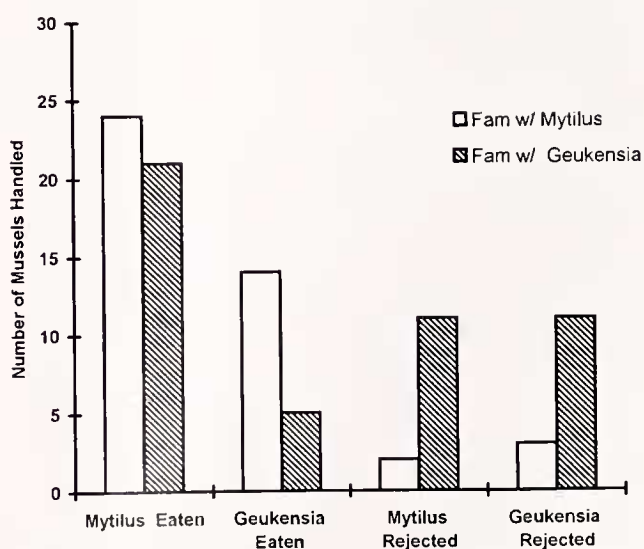

Figure 4. Comparison of total number of prey eaten and rejected by crabs familiarized with *Mytilus* and *Geukensia*. No differences were found in ratios. Abbreviations: Same as in Figure 3.

A chi-square analysis of a 2×2 contingency table determined that the ratio of *Mytilus* to *Geukensia* eaten was not different ($P > 0.05$), nor was there a difference between the ratio of mussel species rejected ($P > 0.05$) for each of the familiarization groups (Table 1). Regardless of the mussel species that the crabs were familiar with, they ate and rejected the same proportion of mussel species.

Discussion

Our results show that, in the absence of recent experience, *Cancer irroratus* did not strongly respond to the effluent of either *Mytilus edulis* or *Geukensia demissa*. Exposure to one prey type increased the sensitivity of the crabs to that prey's odor, and responsiveness increased with experience. The results of the sequential presentation tests indicated a significantly increased sensitivity towards familiarized prey. Scores of low-sensitivity behaviors were higher for familiar effluents than for unfamiliar effluents. However, the simultaneous presentations could not distinguish the responses to the two odors because it was not possible to determine which odor was eliciting the heightened behaviors.

Crabs did not often approach the effluent source in either the sequential or simultaneous tests. These results may be misleading since crabs did react to the odors. The use of prey effluents instead of live prey can influence observed behaviors, because the lack of reinforcement with actual prey may have been responsible for the observed decreases in response.

It is also possible that the concentrations of stimulatory compounds may have been below the thresholds necessary to initiate search or approach. The amino acids glycine, taurine, glutamate, serine, and threonine have been found to be the most stimulatory in feeding assays in several species of *Cancer* (Case, 1964; Allen *et al.*, 1975). These amino acids may have been present at low concentrations in test-mussel metabolites. *Palaemonetes pugio*, a grass shrimp, specifically recognizes various foods by qualitative and quantitative differences in combinations of low molecular weight substances intrinsic to those foods (Carr, 1978).

Concentrations that elicited antennular responses may have been too low for activation of approaches and feeding behaviors. Rebach *et al.* (1990) found antennular sensitivity for mussel extract in *C. irroratus* to be as low as 10^{-10} g l^{-1}. Pearson *et al.* (1979) found similar sensitivities for littleneck clam extract in *C. magister*. Both of those studies used tissue extracts, whereas this study used prey rinse (body odor) from intact animals. The threshold to elicit feeding is 10^5 higher than the arousal threshold in rock crabs (Rebach *et al.*, 1990) and 10^{10} to 10^{17} times higher in blue crab (*Callinectes sapidus*; Ache, 1982). Arousal thresholds are found at concentrations of picograms (10^{-12} g) per liter, search behavior thresholds at micrograms (10^{-6}

g) per liter, and handling and ingestion of food at milligrams (10^{-3} g) per liter (McLeese, 1973; Mackie, 1973; Pearson and Olla, 1977; Ache, 1982). The effluents used in this study did not often direct the crabs' responses towards familiar effluents, but did arouse them. We may therefore infer that these effluents had concentrations between 10^{-12} and 10^{-3} g l^{-1}.

The stomach contents of rock crabs indicate that they are opportunistic feeders (Drummond-Davis *et al.*, 1982). An assortment of algae, polychaetes, gastropods, mussels, and bits of hermit crabs and other crustaceans are typically consumed. It is possible that nutritional needs were not being met by a diet restricted to a single food for an extended time, and the crabs may have lost interest in familiarized prey. Again, feeding reinforcements were absent and may have counteracted the effects of training.

In the foraging tests, tactile and visual cues were introduced by the use of living prey rather than effluents. Both groups of familiarized crabs ate and rejected similar numbers of mussels, and there was no difference in the ratios of *Mytilus* to *Geukensia* eaten and rejected. However, even though crabs encountered both species of mussels, they handled *Mytilus* first, ate *Mytilus* first, and consumed more *Mytilus* than *Geukensia* regardless of familiarization group. Since crabs walked over both species before selecting any prey, both species should have had an equal chance to be handled. *Geukensia* has a heavier shell than *Mytilus*, possibly making it more difficult to open, but this did not account for the crabs' preference, because equal numbers of both species were rejected. Metabolites from both species were present in the test tank. As soon as a mussel was eaten, freshly killed prey odors would have filled the tank, possibly decreasing the importance of odor in choosing the next prey, and other cues may have become more important.

If crabs use more than one sensory cue in prey choice, a hierarchy may exist for all sensory functions in determining prey selection. Maynard and Sallee (1970) found that chemotactile stimulation of lobster dactyls overrode antennular stimulation. Our tests were run in the light to permit videotaping, so visual cues might have played a role in prey selection. *Geukensia* was difficult to see against the mottled calcite, whereas the blue-black colored *Mytilus* contrasted well with the background. Arthropod compound eyes are adept at discerning contrasts (Evans, 1984). *Mytilus* may have been visually less cryptic and thus more susceptible to predation.

The crabs were more likely to have been in contact with *Mytilus* than with *Geukensia* before they were caught, and might have retained their sensitivity for that species. Alternatively, *Mytilus* may have been easier to open, or may have simply tasted better than *Geukensia*. Lobsters are also able to detect differences between two closely related mussels—in this case *Mytilus* and *Modiolus*—and showed increased sensitivity with experience and training (Derby and

Atema, 1981). Atema *et al.* (1980) found qualitative differences in the amino acid content of live prey rinses. The foraging study supported the differences found in sensitivities between crabs familiarized with *Mytilus* and crabs familiarized with *Geukensia*. However, *Mytilus* appeared to be more attractive than *Geukensia* when crabs were given a choice between live prey.

The responses of crabs to mussel odors before and after experience with those mussels indicated that familiarization increased sensitivity towards a prey item. Whether this resulted in the formation of a chemosensory search image or a species-specific preference is not clear. However, recognition and remembrance of familiar prey odors facilitates the location of suitable prey in a benthic habitat where few other cues are available.

Acknowledgments

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